THE PERSISTENCE OF ROLE IN EXTERIOR WORKERS OF THE HARVESTER ANT, *POGONOMYRMEX BADIUS*

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The social organization of an ant colony channels individuals into particular tasks, so that the colony continues to perform its tasks in a regular way. In other words, the colony is organized so that certain roles (*sensu* Oster and Wilson 1978), vital to its function, continue to be filled. The present study reports on role behavior in exterior workers of the harvester ant *Pogonomyrmex badius.*

Three questions are addressed: 1) In *P. badius,* do particular groups of ants consistently do certain tasks? 2) Does the task performed by an ant depend on its age? Because *P. badius* workers live for about a year (Porter and Tschinkel 1982), marked individuals were observed for a longer time (up to four months) in the present study than in previous studies of *Pogonomyrmex* species (Hölldobler 1976, Porter and Jorgensen 1981). 3) Does the task performed by an ant depend on its size? *P. badius* is the only polymorphic species in its genus. Since majors rarely emerged from the nest, only the role behavior of minor workers was considered in this study. However, even within the minor subcaste of *P. badius,* a greater size variation exists than in other *Pogonomyrmex* species. The relationship between size and role in *P. badius* minors is investigated.

In the present study, the behavior of exterior workers is classified into a more detailed set of tasks than in previous studies of the genus. Foraging, i.e. food retrieval, is only one of five activities observed outside the nest. The classification of tasks used here is needed to explain other aspects of *Pogonomyrmex* behavior (Gordon 1983a and b).

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Methods

All experiments were conducted in the laboratory with five queen-right colonies of *P. badius,* each containing about 650 workers. The presence of brood inside the nest could not be ascertained. Colonies were kept in soil-filled tanks (45 × 25 × 20 cm), and fed with Bhaktar-Whitcomb diet (1970), which was placed on the soil surface in a small dish. Individual ants were marked with Testors Gloss Enamel, each with a drop on the top of the head. Single ants were kept isolated overnight after being marked, and then put back into the home colony. No adverse reactions to the marking procedure were observed.

All tasks performed by ants outside the nest were classified into the following five activities (Table 1): Foraging, Nest Maintenance, Patrolling, Midden Work, and Convening. Ants inside the nest were not considered in this study. No majors were marked, since they spent almost all of their time inside the nest, probably assisting in brood care (pers. obs.).

An observation record consisted of the numbers of marked and unmarked ants in each of the five categories of behavior. Observations were made between 8:00 and 20:00. Each observation lasted 5–10 minutes, depending on the total number of ants outside the nest. At least one hour elapsed between successive observations.

A. *Continuity of role.* In each of the five colonies, ants collected while performing one of the five categories of behavior were removed from the colony and marked. For example, in one colony only foragers were marked, in another only patrollers were marked, and so on. In each colony, five ants were marked every five days until 20 ants had been marked. Each group of five ants was marked with paint of a different color. Thus each colony was observed for a total of 35 days, which I call the first observation period. During this time, a total of 728 observations were made, about 145 observations on each colony.

The data were analysed separately for each colony as follows. First, a two-way chi-squared procedure with four degrees of freedom (Sokal and Rohlf 1981) was used to test whether the distribution of the ratio of marked to unmarked ants depends on activity. Next, another chi-squared test, this time a two-by-two test with one degree of freedom, was performed. The latter tested whether ants were significantly likely to continue doing the activity they were doing when marked, called the "tagged activity." Both tests used the total

Table 1. Classification of activities of exterior workers of *P. basius* in laboratory colonies

Foraging	A. Standing at the food dish, eating.
	B. Taking food items into nest.
	C. Piling sand on food.
Nest Maintenance	A. Carrying sand out of nest, putting it down and going back into nest.
	B. Rearranging sand on terrarium surface.
Patrolling	A. Walking around edge of terrarium, inspecting sides with antennae.
	B. Walking around with abdomen tucked under thorax, with frequent stops and changes of direction.
	C. Pawing at sand with front legs and inspecting the resulting small depression with antennae.
Midden Work	A. Repiling midden.
	B. Standing on midden.
	C. Carrying objects (dead ants, food bits, twigs, etc.) to midden.
Convening	A. Standing with a group, grooming each other.
	B. Standing with a group, self-grooming.
	C. With a group milling around slowly under the lamp, sometimes inspecting others of the group with antennae.

numbers of marked and unmarked ants observed in each activity, during the entire observation period. The latter, two-by-two test used the total numbers of marked and unmarked ants observed in the tagged activity, and the two summed values for the other four activities.

B. *Death rates of marked ants.* To determine whether death rate differed according to activity, the colony middens were inspected daily during the first observation period, and dead marked ants were counted.

C. *Continuity of role after a two-month interval.* The observations described in part A were ended on July 12, 1982. On September 12, 1982, observations of the same marked individuals in the same five colonies were begun again and continued for 25 days, which I call the second observation period. A total of 193 observations were made, and the data were analysed as before.

D. *Behavior of callow workers.* Adult ants that have recently emerged from the pupal stage, or callows, are lighter in pigment than older adults. Their behavior was examined in two ways. First, for 25 days during the second observation period, the number of callows in each of the five activities was recorded, as well as the numbers of all other ants. Records were obtained on only two colonies, since the other three colonies had but few callows outside the nest. These data, consisting of 81 observation records, were analysed as in Part A with a two-way chi-squared procedure. This tested whether the distribution of the observed number of callows depended significantly on activity.

Second, 20 convening callows in one colony were marked, using the procedure described in part A. They were observed for 40 days, beginning with the day on which the first group of five callows was marked. Convening callows were chosen because it was rare for a callow to be seen doing any of the other four activities. A total of 149 observations were made in this procedure. The data were analysed as in parts A and C.

E. *Relation of body size to activity.* To determine whether body size is correlated with activity, the head widths of 25 minors in each of 7 colonies, a total of 175 ants, were measured. Each group of 25 ants consisted of 5 ants from each of the five categories of behavior, or activities. Head width was measured at right angles to the line between the clypeus and occiput, immediately posterior to the eyes,

using an ocular micrometer calibrated in 0.1 mm. Measurements were estimated to the nearest 0.01 mm. The data were subjected to a two-way analysis of variance (Sokal and Rohlf 1981), which tested for the effect of activity and colony of origin on head width and for a colony-activity interaction.

Results

A–C. *Continuity of role.* In both observation periods, the ratio of marked to unmarked ants depended highly significantly on activity in all five colonies (two-way chi-squared test, $p < 0.0001$ for all tests). Table 2A shows the data from the first, 35-day observation period (part A). The deviations shown are based on the expected values derived in the two-way test for each colony. The significance values along the diagonal of the table are the result of the two-by-two chi-squared tests of whether marked ants continued to do the tagged activity. These results all show highly significant, positive deviations from the expected values. All groups of ants continued doing the activities that they were doing when marked. Thus, the data of Table 2A show that groups of ants do specialize in certain activities.

Cells not on the diagonal in Table 2A show the data for ants in the four activities other than the tagged one. In some cases, the data show a large positive deviation from the expected value in an activity other than the tagged one. This indicates that marked ants were likely to perform a second activity as well as the tagged one. The results shown in Table 2A, and summarized in Table 2C, lead to the following conclusions.

Ants marked while doing midden work tended to be later engaged in patrolling, and vice versa, indicating that midden work and patrolling are done by the same ants. Ants marked while convening later did midden work as well. But ants marked doing midden work did not later do convening. Similarly, ants marked while doing nest maintenance later did patrolling as well. But ants marked while patrolling did not later do nest maintenance. These results suggest that ants marked while convening were in transition to midden work, and that ants marked while doing nest maintenance were in transition to patrolling. In these two colonies, I examined the proportions of marked ants doing each activity as a function of time in the course of the first observation period, but saw no interesting or possibly significant changes in these proportions. The possibility of later role

changes of ants marked while convening or doing nest maintenance is discussed below.

The numbers (each out of 20) of dead marked ants in the first observation period were as follows: midden workers, 11; patrollers, 16; foragers, 2; conveners, 1; nest maintenance workers, 2.

Table 2B shows the data from the second, 25-day observation period, begun two months later. Several obvious differences between the data of Table 2A and that of Table 2B should be noted. Fewer observations (149) were made in the second observation period than in the first one (728). The colony in which patrollers were marked was barely active during the second observation period, for unknown reasons. Colony inactivity was not accompanied by any obvious increase in the number of dead workers visible in the midden. Because no marked ants were observed, it was not possible to analyse the data from this colony. As noted above, many midden workers and patrollers died during the first observation period. Though only two marked foragers died during this first 35-day period, the number of marked foragers had decreased two months later, indicating that many foragers died during the interval between the first and second observation periods.

The two-by-two tests for the second observation period show that marked ants were no longer likely to do the tagged activity. All marked ants had either died or changed activity after a two-month

Table 2(A–D). Behavior of marked ants
(Pages 000–000)

In Tables 2A and 2B, each row of the matrix shows the results from one colony, in which ants were marked doing the indicated activity. The first five columns show the subsequent activities of marked ants. In each cell are shown the total numbers of marked and unmarked ants observed during the entire observation period, the deviation from the expected value, and the percent deviation (of the expected value). **means $p < 0.001$; NS means "not significant." The last column shows the mean number of marked ants per observation.

Table 2C summarizes Tables 2A and 2B. It shows the results of the two-by-two chi-squared tests of whether marked ants continue doing the tagged activity. Also shown are strong positive deviations from expected values in other activities. Plus and minus signs indicate the sign of the deviations from expected values. As in Tables 2A and 2B, each row of the matrix shows the results from one colony, in which ants were marked doing the indicated activity.

Table 2D is similar to Tables 2A and 2B. It shows the data from part D, in which callow ants were marked when convening.

Table 2A. Behavior of marked ants during first observation period.

Activity When Marked		*Subsequent Activity* F	NM	PT	MW	CN	Mean no. marked ants seen per observation
F		**					2.28
	Marked	47	126	26	16	29	
	Unmarked	309	1397	281	373	568	
	Dev. for Exp.	+19.6	+8.8	+2.4	−13.9	−16.9	
	% Dev.	.72	8	10	46	36	
NM			**				5.60
	Marked	37	436	116	134	184	
	Unmarked	623	4755	1112	2764	2915	
	Dev. for Exp.	−8.8	+75.9	+30.8	−67.0	−31.0	
	% Dev.	19	21	36	33	14	
PT				**			2.18
	Marked	23	34	123	173	48	
	Unmarked	397	2776	904	1736	1309	
	Dev. for Exp.	+0.6	−115.8	+68.3	+71.2	−24.3	
	% Dev.	3	77	125	69	34	
MW					**		7.05
	Marked	9	67	102	343	276	
	Unmarked	242	1514	819	1840	4688	
	Dev. for Exp.	−11.2	−60.3	+27.9	+167.3	−123.6	
	% Dev.	55	47	38	95	30	
CN						**	6.57
	Marked	50	325	131	245	313	
	Unmarked	404	2481	701	1124	1362	
	Dev. for Exp.	−17.7	−93.4	+6.9	+40.9	+63.3	
	% Dev.	26	22	6	20	25	

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Table 2B. Behavior of marked ants during second observation period

		NS					
F	Marked	11	3	29	32	91	0.64
	Unmarked	130	458	566	557	721	
	Dev. for Exp.	+2.0	−26.5	−9.0	−5.6	+39.1	
	% Dev.	22	89	24	15	75	
			**				
NM	Marked	11	8	133	41	5	3.94
	Unmarked	264	925	1289	994	937	
	Dev. for Exp.	−0.8	−32.1	+71.9	−3.5	−35.5	
	% Dev.	7	80	118	8	88	
PT	Marked	0	0	0	0	0	0
	Unmarked	7	12	13	15	0	
	Dev. for Exp.	–	–	–	–	–	
	% Dev.	–	–	–	–	–	
					**		
MW	Marked	4	2	41	11	67	0.74
	Unmarked	76	136	360	417	165	
	Dev. for Exp.	−3.8	−11.5	+1.8	−30.8	+44.3	
	% Dev.	48	85	5	74	195	
						NS	
CN	Marked	23	4	46	40	12	2.23
	Unmarked	128	375	488	529	192	
	Dev. for Exp.	+12.7	−21.8	+9.7	+1.3	−1.9	
	% Dev.	55	84	26	3	14	

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Table 2C. Summary of results from first and second observation periods

	First Observation Period				
Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
F	** +				
NM		** +			+
PT			** +	+	
MW			+	** +	
CN				+	** +

	Second Observation Period				
Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
F	NS				+
NM		** −	+		
PT					
MW				** −	+
CN	+		+		NS

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

interval. Ants originally marked while convening now appeared to do foraging instead. Ants marked while doing midden work now did convening, as did those marked while foraging. Finally, ants marked while doing nest maintenance now tended to do patrolling. These results are summarized in Table 2C.

D. *Behavior of callow workers.* The two-way chi-squared test on the data on callow workers shows that the ratio of callows to other ants depends highly significantly on activity ($p < 0.0001$). In both colonies in which callows were observed, the callows were most often observed convening.

Callows that were marked while convening and observed for 35 days were significantly likely to continue to convene ($p < 0.0001$ for two-way chi-squared test, $p < 0.001$ for two-by-two chi-squared test) (Table 2D). Although dark-pigmented, older ants marked while convening were also likely to do midden work during the first 35 days (Table 2A), it appears that convening callows were *not* likely to do midden work (Table 2D).

The results of these two procedures show that callow ants convene for at least 35 days. Although in the field *P. badius* callows acquire darker, adult coloration within 25 days (Gentry 1974), only 6 of the 20 callows marked while convening were as dark as non-callow adults at the end of 40 days. The others were still of intermediate coloration.

E. *Body size.* There was no significant relationship between head width and type of activity in minor workers. The two-way anova showed no interaction between colony of origin and type of activity ($DF = 24$, $SS = 0.44$, $F = 0.64$, $p > 0.8993$), no effect of type of activity on head width ($DF = 4$, $SS = 0.09$, $F = 0.77$, $p > 0.5492$), and a significant effect of colony of origin on head width ($DF = 6$, $SS = 1.30$, $F = 7.53$, $p > 0.001$). Mean head size for all 25 workers in all five activities ranged from 1.53 mm in one colony to 1.78 mm in another of the seven colonies. Mean worker size increases with colony age (Oster and Wilson 1978). Differences in age among the seven colonies probably account for the effect of colony of origin on head width.

Discussion

At any one time, exterior workers in the *P. badius* colony can be divided into four groups that consistently perform certain roles for at least 35 days: 1) midden work and patrolling, 2) nest maintenance, 3) foraging, and 4) convening.

Table 2D. Behavior of callows while convening

	Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
						**
CN	Marked	26	17	63	74	385
	Unmarked	2290	14382	4664	9731	15601
	Dev. for Exp.	−1.7	−155.2	−6.5	−43.3	+193.8
	% Dev.	6	90	12	37	101

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Convening of exterior workers is observed much more often in the laboratory than in the field. Convening includes resting and mutual grooming. It probably serves a thermoregulatory function as well, because convening ants in laboratory colonies always gather in the warmest place on the terrarium surface, directly underneath a lamp. Convening has been observed in field colonies of *Pogonomyrmex,* but only rarely (MacKay 1981; Gordon 1983b, 1984a, b). It is possible that, in the field, convening is usually done inside the nest where conveners would be less subject to predation.

The results of this study, summarized in Table 2C, suggest the diagram depicted in Figure 1. The diagram shows how role may depend on worker age in exterior workers of *P. badius.* It should be emphasized that the diagram is hypothetical, pending further investigation, and that it rests on two assumptions. In keeping with results on many other species (Wilson 1971), it is assumed that younger ants first work inside the nest, then work outside the nest for the remainder of their lives. Another assumption is that in the laboratory experiments reported on here, the death rate of ants in a particular activity depends on their age rather than on the hazards or energetic costs associated with their activity. Convening ants are clearly less active than ants in the other four activities (see Table 1). However, there is at present no empirical basis for distinguishing the other four activities in terms of the energy expended performing them.

Ants doing midden work and patrolling are shown as the oldest in Figure 1, because ants marked while doing these activities died within

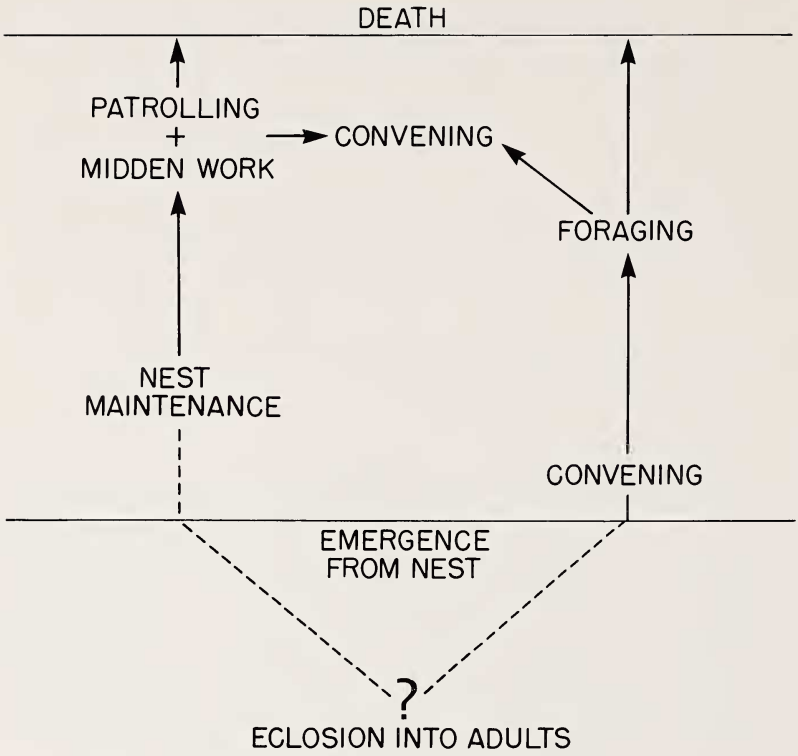

Fig. 1. How role depends on age in exterior workers of *P. badius*. The vertical direction represents worker age.

35 days, sooner than ants in any of the other groups. It seems that convening is done at two different times in the life of *P. badius* individuals. One group of conveners is the youngest group shown, because callows are most likely to convene, and continue to do so for at least 35 days. The results from the second observation period suggest that convening ants become foragers, and some foragers later become conveners, as shown. Since marked midden workers did convening in the second observation period, an arrow is drawn from the patrolling and midden work group to the older convening group. There is evidence that this transition may also be made in the opposite direction: some ants marked while convening (not callows —see Part A) did midden work in the first observation period, and patrolling in

the second. Marked nest maintenance workers were probably in transition to patrolling during the first observation period. Later, nest maintenance ants became patrollers, as shown.

The results of Porter and Jorgensen (1981) for *P. owyheei* suggest a schema similar to the one of Figure 1. Foraging, for these authors, may include midden work, patrolling, convening and foraging as they are defined in Table 3. By examining the behavior of foragers in more detail, the present study indicates the existence of at least one group of ants older than those engaged in food retrieval: ants doing both midden work and patrolling. The relationship between these two activities will be addressed in a subsequent paper (Gordon 1984b). It would be interesting to examine role behavior in field colonies of *P. badius* using the classification of behavior employed in the present study.

I do not attempt in this study to describe division of labor in the *P. badius* colony as a whole, because the behavior of interior workers is not considered. But the results raise several questions about age polyethism in exterior workers. First, there appear to be two groups of exterior workers in the colony. Ants of one group first do convening and then foraging, while ants of the other first do nest maintenance and then midden work and patrolling. It appears that ants from either group may then become conveners. What determines to which group an ant will belong? The possibility that these groups correspond to different sizes of workers within the minor subcaste was examined, but I found no such relationship. Second, exactly how long do individual ants remain in each of their roles? For a long-lived species like *P. badius,* the answer to this question awaits a marking technique better than the one used in this study. After about four months, some of my marked ants were seen to have most of the paint chipped off.

The unresolved questions in this study are part of a larger one: how is the distribution of workers into different roles regulated? There is considerable evidence that individuals are channelled into particular roles according to the current needs of the colony (e.g. Meudec and Lenoir 1982, Lenoir and Ataya 1983, Wilson 1983). To answer the questions raised by this study, we must come to understand the system by which the colony assesses and predicts what needs to be done.

Summary

Exterior workers in laboratory colonies of the southern harvester ant, *Pogonomyrmex badius,* were marked while performing one of the following: 1. midden work, 2. patrolling, 3. nest maintenance, 4. convening, or 5. foraging. These activities were consistently performed by marked ants for at least 35 days. The results indicate that the five activities are performed by four distinct groups of ants; it appears that midden work and patrolling are done by the same ants. Three months after marking, conveners had become foragers, and nest maintenance workers had become patrollers. Younger, callow ants were most often observed convening. Midden workers and patrollers died sooner than other marked ants. These results show how role may depend on worker age. In this species the minor caste is continuously polymorphic, but no evidence for size polyethism within the minor caste was found.

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